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The mandibular gnathal edges: Homologous structures throughout Mandibulata?

by

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ABSTRACT

Increasing evidence, in particular from gene expression data, indicates that mandibles throughout the Mandibulata are gnathobasic and that myriapod and hexapod mandibles do not represent 'whole limbs'. These observations do not necessarily imply that the gnathal edges of the mandibles are also homologous, though this homology finds some support from gene expression. The gnathal edges of mandibles commonly consist of three parts: an incisor process (*pars incisivus*), a molar process (*pars molaris*) and a *lacinia mobilis* (or similar structures with different names), situated between the two processes. A comparative SEM study shows that, in contrast to the *lacinia mobilis*, a broad homology of the *pars incisivus* and the *pars molaris* in Myriapoda, Crustacea and Hexapoda can potentially be defended. In Chilopoda, the proximal part of the gnathal edge is represented by a bristled pad, the 'Haarpolster', that has been identified as equivalent to a *pars molaris*. By comparison to other myriapods, notably Symphyla, Scutigeromorpha is assumed to be plesiomorphic in having the Haarpolster on a separate sclerite and in having a molar plate formed by rows of confluent spines amidst the Haarpolster bristles. In many crustacean and hexapod mandibles, the surface of the *pars molaris* is covered by a pattern of scaly transverse ridges built by rows of spines, often confluent with each other and with projections of the gnathal edge. This implies that the grinding surface of the *pars molaris* is not the original surface of the gnathal edge, but is built on a more distal second level. Rows of spines and a spinose marginal fringe with gaps between the rows are common features of the *pars molaris* in myriapods, hexapods and crustaceans, providing evidence for homology by special structure, in addition to the criterion of positional correspondence.

INTRODUCTION

The homology of mandibles in myriapods, hexapods and crustaceans is central to the theory that these arthropods are united as a monophyletic group, the Mandibulata (Snodgrass 1938 1950). A challenge to the homology of mandibles figured prominently in Tiegs & Manton's (1958) arguments for arthropod polyphyly (described in detail in Manton 1964 1977). According to the polyphyleticists, crustacean mandibles are gnathobasic in origin, whereas myriapod and hexapod mandibles bite with the tips of whole limbs. This theory of different origins of mandibles was rejected by Lauterbach (1972), Boudreaux (1979), and Weygoldt (1979), who reasoned that the positional equivalence of mandibles is most consistent with a single origin, and that myriapod mandibular musculature is coxal (as implied by a gnathobasic origin) rather than being that of a telopodite (as implied by a 'whole limb' origin). The homology of mandibles can be defended on classical morphological grounds: mandibles are the appendage of the first post-tritocerebral segment; they are the anteriormost mouthpart of the adult head; mandibles are embedded in a chewing chamber beneath the labrum, and they have a coxal endite used for food manipulation (Wägele 1993; Bitsch 2001).

In comparative studies of Arthropoda, gross structure, musculature and function of the mandible have received considerable attention, but the detailed structure of the mandibular gnathal edge presents several unsolved problems. In this study, we explore the comparative morphology of the gnathal edge of mandibles in myriapods, crustaceans and hexapods. Evidence is marshalled for the homology of the molar and incisor parts into which many mandibles are differentiated. In particular, we attempt to determine the identity of certain problematic structures on the gnathal edge of myriapod mandibles, such as the so-called Haarpolster of Chilopoda.

Gene expression and homology of mandibles

Recent expression data for the Homeobox gene *Distal-less* (*Dll*), which plays an important role in arthropod limb development, as well as for *dachshund*, suggest the assumption of homology of the mandibles throughout the Mandibulata (e.g. Panganiban *et al.* 1995; Popadić *et al.* 1996 1998; Scholtz *et al.* 1998; Scholtz 2001; Prpic *et al.* 2001). These findings, which are consistent with monophyly of Mandibulata, are implicitly rejected in several recent molecular studies that have allied myriapods with chelicerates rather than with hexapods and crustaceans (Cook *et al.* 2001; Hwang *et al.* 2001; Kusche & Burmester 2001, but see Kusche *et al.* (2002) for support for the Mandibulata).

In crustaceans that develop a mandibular palp, *Dll* expression appears in the early limb bud, but is restricted in more advanced stages to the region of the outgrowth of the mandibular palp. In Crustacea that lack a palp, e.g. terrestrial isopods such as *Porcellio scaber* Latreille, 1804, *Dll* expression starts early but the expression is restricted during development of the limb bud to an area that can be interpreted as a vestigial anlage of the palp. In the diplopod *Glomeris marginata* (Villers, 1789), *Dll* has only a temporary expression in a lateral position, which can also be interpreted as the vestigial anlage of a palp (Scholtz *et al.* 1998). The conclusion is that in adult myriapods, no distal parts of the mandible are present, and therefore the mandible does not represent a whole limb with telopodite. In the hexapods studied, *Dll* expression is totally absent, which implies that even a vestige of a palp is lacking (e.g. Panganiban *et al.* 1995; Popadić *et al.* 1996 1998; Scholtz *et al.* 1998). Thus, the expression pattern of *Dll* is consistent with the hypothesis that myriapod and hexapod mandibles are gnathobasic like those of crustaceans. This finds some additional support from the expression of *dachshund* in the beetle *Tribolium castaneum* (Herbst, 1797) (Prpic *et al.* 2001). Based on the similarity in size and expression of *dachshund* in all three gnathal appendages in mutant embryos for *Tc' Dll*, the authors endorsed a serial homology of the entire mandible with the coxal parts of the maxilla and labium, and the coxa of the legs.

Although we now have evidence for gnathobasic mandibles in all mandibulate groups, this evidence does not necessarily imply that the gnathal parts of the mandibles in myriapods, hexapods and crustaceans are always formed by a homologous part of the protopod. Support, however, for the homology of the gnathal edges of the mandibles in crustaceans, myriapods and hexapods is provided by the total absence of *Dll* expression in the *corpus mandibularis* that includes the gnathal edges in advanced stages of embryonic mandibles (Scholtz *et al.* 1998; Scholtz 2001; Richter 2002). If any (transitory) expression of *Dll* in the mandibles exists, this expression is restricted to an area that can be interpreted as the anlage of the palp. In contrast, *Dll* might be expressed in the inner lobes of the maxillula and other limbs (Scholtz 2001; Richter 2002). This difference in the *Dll* expression pattern between mandibles and more posterior limbs provides evidence for the homology of the mandibles in all mandibulates.

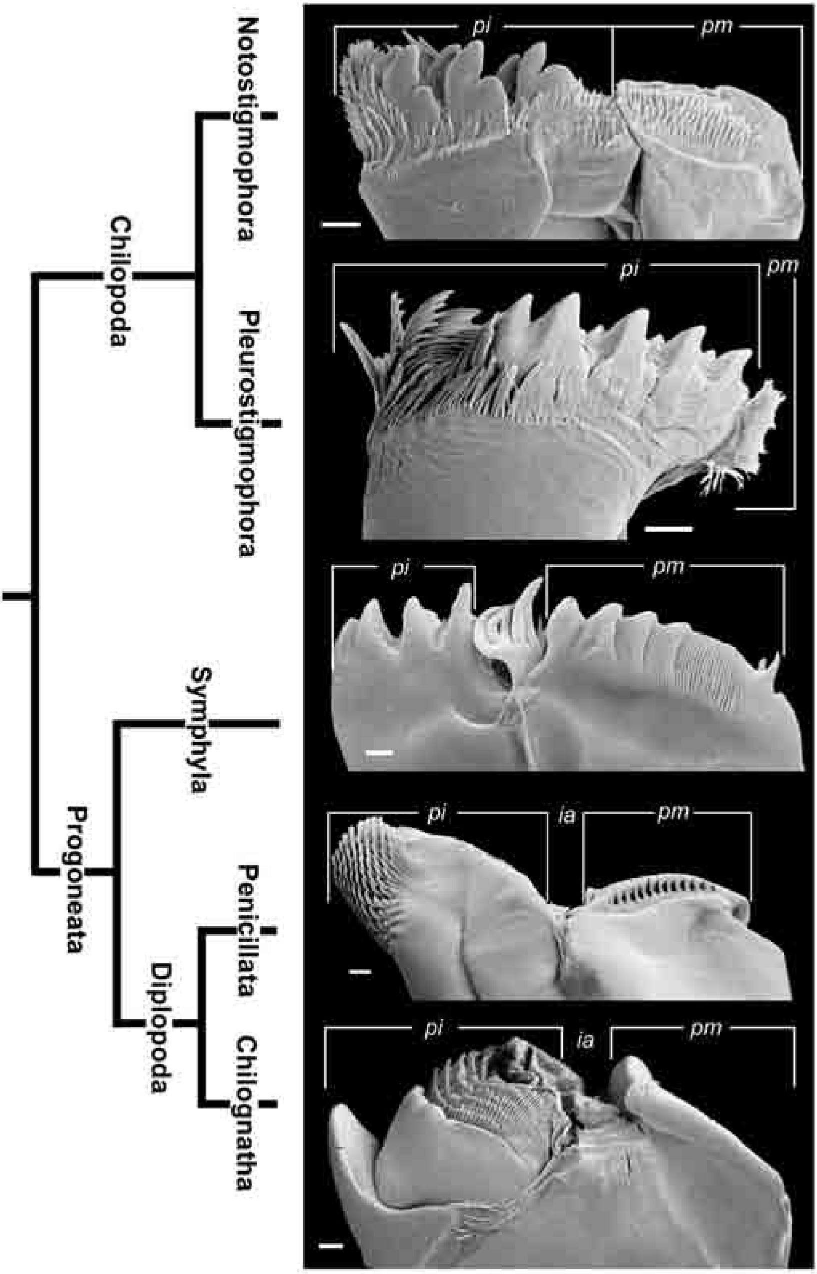
Notostigmophora
Pleurostigmophora
Chilopoda
Symphyla
Progoneata
Penicillata
Chilognatha
Diplopoda
pi
pm
ia

Fig. 1. Mandibular gnathal edge in Myriapoda, showing limits of *pars incisivus* (*pi*) and *pars molaris* (*pm*). All are left mandibles. Species are *Parascutigera* sp. [Notostigmophora, scale 50 µm], *Cryptops spinipes* [Pleurostigmophora, scale 50 µm], *Hanseniella* sp. [Symphyla, scale 5 µm], *Unixenus mjobergi* [Penicillata, scale 10 µm] and *Cladethosoma clarum* [Chilognatha, scale 60 µm]. The intermediate area (*ia*) is indicated in Diplopoda. The cladogram is depicted with Myriapoda monophyletic.

The *pars molaris* and *pars incisivus*

In this paper, we define the essential parts of the mandibular gnathal edge as follows: the *pars incisivus* is the distal part of the mandibular gnathal edge that consists of multicusped teeth or their derivatives; the *pars molaris* represents the proximal part (i.e. the part closer to the mouth opening) of the gnathal edge, is generally a grinding surface that includes closely associated (often confluent) spines forming transverse or concentric surficial ridges, and has a marginal fringe of spines. The terms 'molar process', widely used by carcinologists, and 'molar hook' (Kraus 1998 2001) are considered synonymous with *pars molaris*. The term 'molar plate' is used in Diplopoda (Enghoff 1979; Ishii & Tamura 1995), in which it represents the main component of the *pars molaris* ('molar plate' has been similarly applied in Collembola, e.g. by Koch (2001)). Usage of the term 'molar plate' is here restricted to those myriapods in which a discrete plate-like element is differentiated in the *pars molaris*. In diplopods, a so-called intermediate area that bears fringes and/or hair-like or scale-like projections (Enghoff 1979) occurs between the *pars incisivus* and *pars molaris* (Fig. 1).

MATERIAL AND METHODS

Species examined for this study are: Chilopoda - *Scutigerina weberi* Silvestri, 1903; *Parascutigera* sp.; *Paralamyctes* cf. *chilensis* (Gervais *in* Walckenaer & Gervais, 1847); *Lithobius obscurus* Meinert, 1872; *Cryptops spinipes* Pocock, 1891; *Ethmostigmus rubripes* (Brandt, 1840); *Alipes crotalus* (Gerstaecker, 1854); Symphyla - *Hanseniella* sp.; Diplopoda - *Unixenus mjobergi* (Verhoeff, 1924); *Cladethosoma clarum* (Chamberlin, 1920); Hexapoda - *Campodea tillyardi* Silvestri, 1931; *Nesomachilis howensis* Sturm, 1980; *Ctenolepisma* sp.; Remipedia - *Speleonectes* cf. *tulumensis* Yager, 1987; Branchiopoda - *Branchinella pinnata* Geddes, 1981; *Limnadopsis birchii* (Baird, 1860); *Cyclestheria hislopi* (Baird, 1859); *Eurycercus glacialis* Lilljeborg, 1887; Malacostraca - *Paranebalia* sp.; *Meganyctiphanes norvegica* (M. Sars, 1857); *Anaspides tasmaniae* (Thomson, 1892); *Peludo paraliotus* Wilson & Keable, 2002; *Gnathophausia zoea* Willemoes-Suhm, 1875; *Tethysbaena argentarii* (Stella, 1951).

Preparation for the SEM followed standard procedures. The SEMs used were a JEOL JSM-840 at the Zoologisk Museum, University of Copenhagen, a Leo 1430 at the Humboldt University Berlin, and a Leo 435VP using a Robinson backscatter detector at the Australian Museum in Sydney.

RESULTS AND DISCUSSION

Myriapoda

Chilopoda

Koch (2001) and Kraus (2001) have both suggested that the *pars molaris* is transformed in Chilopoda into a hair pad or Haarpolster (*sensu* Verhoeff 1918; = pulvillus of Crabill 1960). The most compelling evidence for the identity of the Haarpolster as a *pars molaris* (or at least the inclusion of a *pars molaris* in the Haarpolster) is seen in Scutigeromorpha. We have examined the gnathal edge of the mandible using SEM in *Scutigerina weberi* Silvestri, 1903, *Allothereua maculata* (Newport, 1844), *Scutigera coleoptrata* (Linnaeus, 1758), and *Parascutigera* sp. (Fig. 1), and observe that details are conservative in all taxa. *Scutigerina weberi* (Fig. 2) serves as the basis for the following descriptive account.

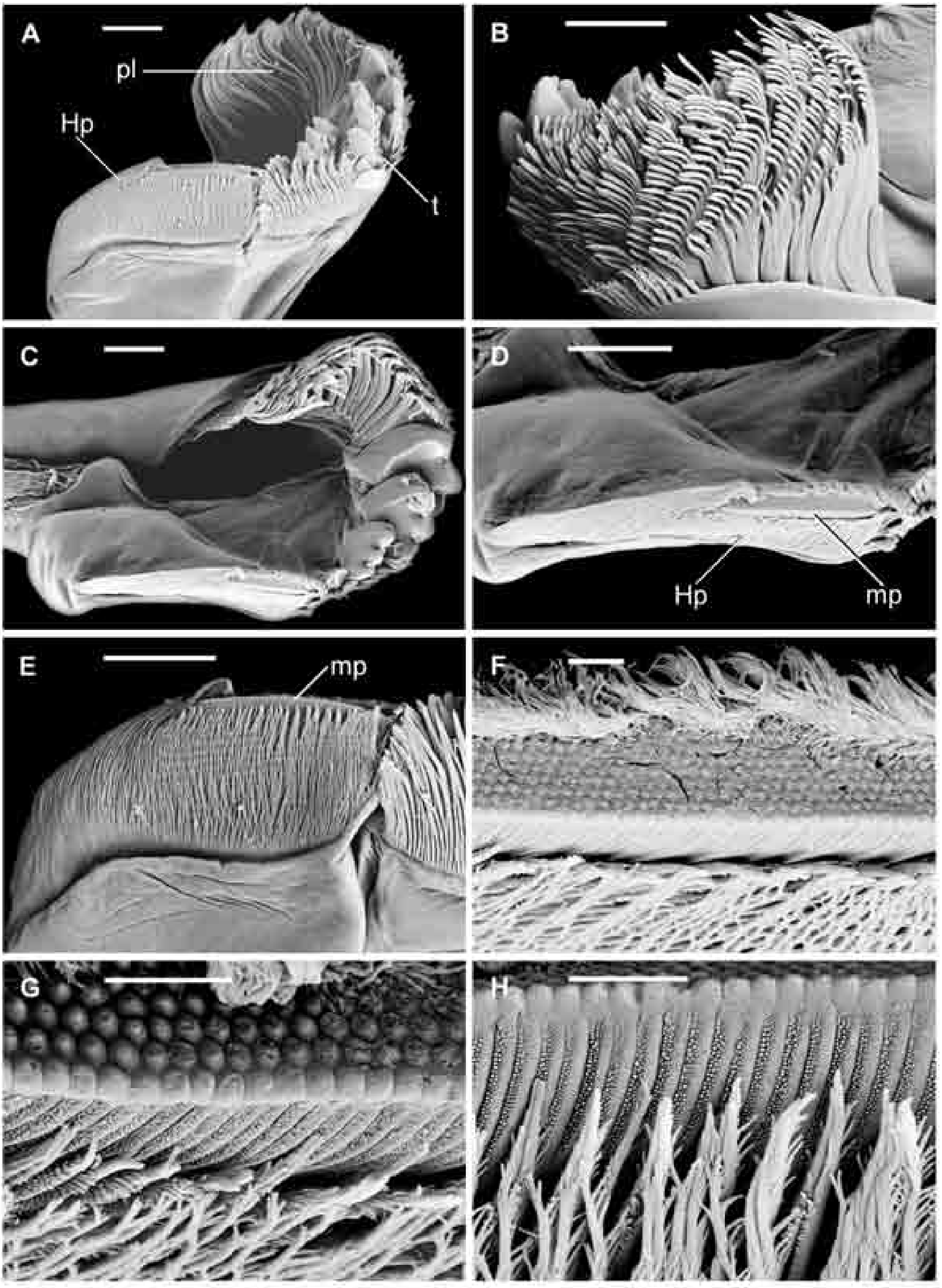

Fig. 2. *Scutigerina weberi* [Scutigeromorpha: Scutigeridae], right mandible. Scales 100 µm (A–E), 10 µm (F–H). A. Gnathal edge, anterior view of Haarpolster (Hp), with *pars incisivus* divided into pectinate lamellae (pl) and cluster of teeth (t). B. Pectinate lamellae. C. Gnathal edge, medial view. D. Haarpolster (Hp), medial view, showing molar plate (mp). E. Haarpolster, anterior view. F–G. Details of molar plate in Haarpolster, medial view. H. Detail of anterior edge of molar plate in Haarpolster, anterior view.

As in all scutigeromorphs, the mandibular shaft in *Scutigerina* is divided into several sclerites, with the Haarpolster occupying a separate sclerite (Figs 1, 2A) from that which bears the dentate lamina (a cluster of three multicusped teeth in all Scutigeromorpha) and, most distally, the pectinate lamellae (pl, Fig. 2A). In *Scutigerina weberi*, about 15 pectinate lamellae are present (Fig. 2B), each composed of up to 28 slender, curved pectinations branching from a common base. Each individual pectination has short spines on both margins along its distal part. As in all scutigeromorphs, the Haarpolster is a long, narrow structure dominated by dense bristles (Figs 2A, D, E). These bristles have short marginal branchings along their length, and are arranged in a few rows along the Haarpolster. Amidst the dense bristles of the Haarpolster is a structure that we identify as a molar plate (mp, Figs 2D–F); proximal to this plate are additional branching bristles. The narrow, elongate molar plate occupies more than half of the total length of the Haarpolster (Fig. 2D). Its gnathal surface is flattened, composed of about 10 rows of rounded tubercles, the tubercles of successive rows alternating in a dense-packing arrangement (Figs 2F–G). On the anterior edge of the plate, fused to the outer (anterior) row of tubercles, is a series of elongate ridges arranged side by side and fused to each other (Fig. 2G–H). These ridges are of similar width to the tubercle rows on the molar plate. The ridges have dense, small tubercles or short papillae along their proximal sides (Fig. 2H). Similar short, dense papillae are seen along the proximal side of the bristles in a bristle row between the ridges on the anterior face of the molar plate and the main fringe of Haarpolster bristles (Figs 2G–H). These papillate bristles, which have short marginal bifurcations like the main fringe of Haarpolster bristles, are morphologically and topologically intermediate between the ridges on the molar plate and the branching Haarpolster bristles. As such, the papillate ridges on the anterior edge of the molar plate may be derived from fused papillate bristles, which themselves are modifications of branching, non-papillate bristles. Furthermore, the correspondence between the papillate ridges and the tubercle rows on the molar plate suggests that the tubercles are themselves derived from fused bristles or spines. These relationships would then allow that the molar plate of Scutigeromorpha incorporates rows of confluent spines.

In contrast to the arguments above for Scutigeromorpha, in many chilopods little evidence other than the positional correspondence (i.e. occupying the proximal extent of the gnathal edge) can be cited to support the identity of the Haarpolster as a *pars molaris*. This is particularly so in Lithobiomorpha and Scolopendromorpha (Fig. 1), in which the Haarpolster is little more than a cluster of bristles proximally on the gnathal edge, and the dentate lamina of multiple paired teeth is expanded along most of the gnathal edge (Figs 3A–D for Lithobiomorpha; Figs 3E–G for Scolopendromorpha). In Craterostigmomorpha (*Craterostigmus tasmanianus* Pocock, 1902), the Haarpolster is a large, densely spinose pad, the spines being multifurcating (Borucki 1996, figs 10, 11; *pers. obs.*). In Geophilomorpha, where sweeping and rasping are associated with the most highly modified mandibles in Chilopoda, the Haarpolster has uncertain identity. It is possibly incorporated into or represented by a large pad of small, dense spines in some taxa (Borucki 1996, figs 8, 9) and is evidently wholly absent in others (Borucki 1996, fig. 7), in which the dentate lamina extends to the proximal edge of the mandible.

If the pectinate lamellae, internal tooth, and external tooth of Diplopoda (see discussion below) are regarded as components of a *pars incisivus* (see above), then the pectinate

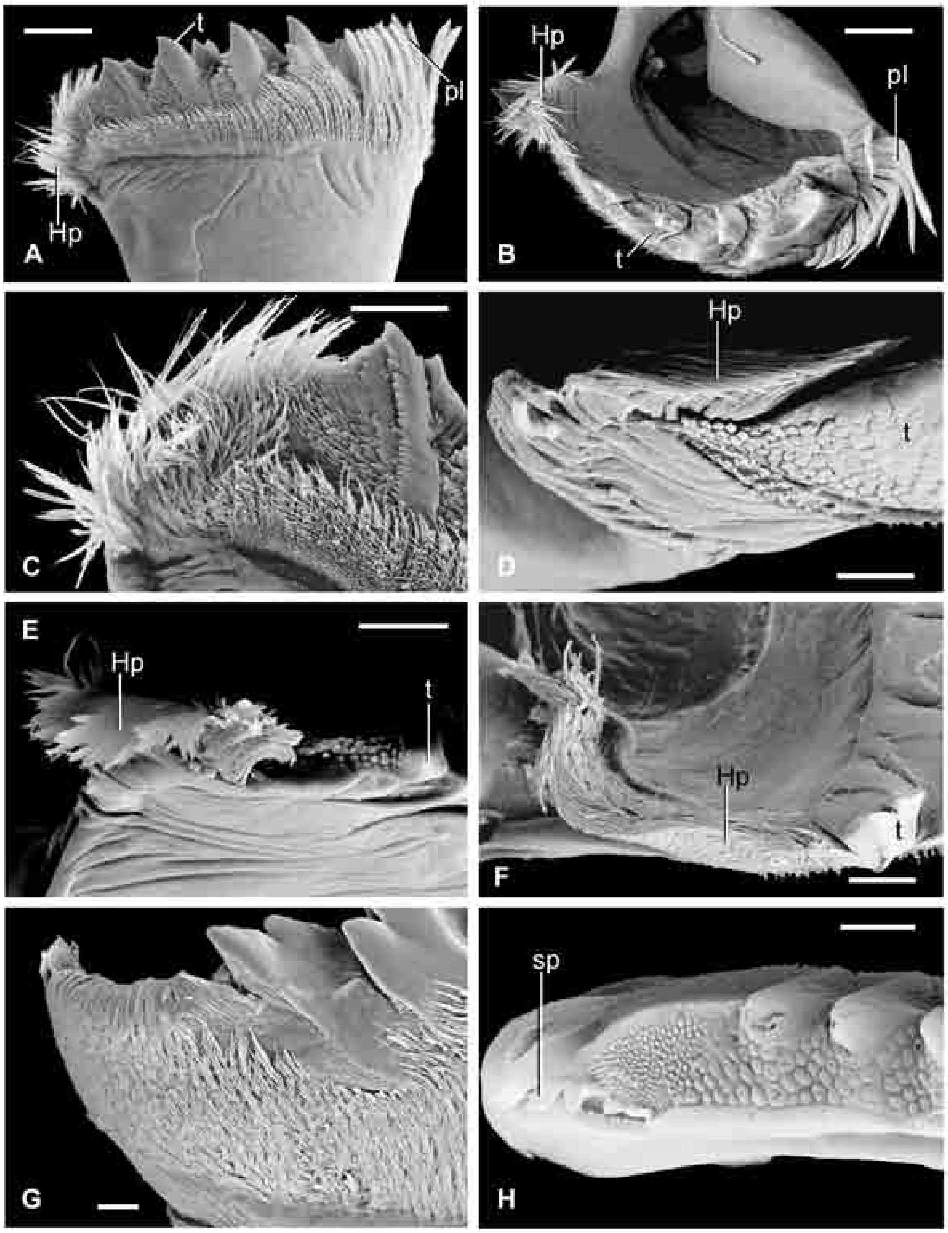

Fig. 3. Mandibular gnathal edge in Pleurostigmophora and Symphyla. All right mandibles except H. A–D, Lithobiomorpha; E–G, Scolopendromorpha; H, Symphyla. A–C. *Paralamyctes* cf. *chilensis* [Henicopidae]. A, B, gnathal edge, anterior and medial views, showing pectinate lamellae (pl), teeth (t) and Haarpolster (Hp), scales 50µm. C. Haarpolster and dorsalmost tooth, anterior view, scale 30 µm. D. *Lithobius obscurus* [Lithobiidae]. Haarpolster (Hp) and dorsalmost tooth (t), medial view, scale 20 µm. E. *Cryptops spinipes* [Cryptopidae]. Haarpolster (Hp) and dorsalmost tooth (t), medial view, scale 30µm. F. *Ethmostigmus rubripes* [Scolopendridae]. Haarpolster and dorsalmost tooth, medial view, scale 30 µm. G. *Alipes crotalus* [Scolopendridae]. Haarpolster and dorsalmost teeth, anterior view, scale 50 µm. H. *Hanseniella* sp. [Scutigerellidae]. Proximal part of *pars molaris* and cluster of spines (sp), medial view, scale 5 µm.

lamellae of Chilopoda can be homologised with at least part of this structure. In particular, the pectinate lamellae of Chilopoda (Figs 1, 2B) may be homologous with the pectinate lamellae of Diplopoda (Edgecombe & Giribet 2002). In both groups, the pectinate lamellae are on the distal part of the mandibular gnathal edge, consisting of multiple comb-like elements, and have a hyaline composition. The dentate lamina of Chilopoda (i.e. the group of three teeth in Scutigeromorpha and *Craterostigmus*, and four or five teeth in Lithobiomorpha and Scolopendromorpha) is more typical in its structure to the *pars incisivus* in hexapods and crustaceans. The expanded series of teeth in Zygentoma (*Lepisma*: Koch 2001, figs 29–31), for example, is comparable to the expanded dentate lamina in lithobiomorphs and scolopendromorphs (as well, the *pars molaris* is shortened in Zygentoma much as its probable homologue, the Haarpolster, is reduced in those chilopods. The scale-like surface of the *pars molaris* in Lepismatidae resembles the intergrading scales and bristles of the Haarpolster in lithobiomorphs: Edgecombe *et al.* 2002, fig. 7).

The conventional concept of Scutigeromorpha as sister group to all other chilopods (Pleurostigmophora) (Edgecombe *et al.* 1999 and references therein) assumes the presence of a molar plate in scutigeromorphs is a plesiomorphic character. This is dependent, of course, on the homology of the structure interpreted above as a molar plate in scutigeromorphs and the molar plate of other myriapods (see argumentation below). If so, a molar plate may be part of the ground-pattern of Chilopoda, being lost in the diminutive Haarpolster of those pleurostigmophorans that expand the dentate part of the mandible (Lithobiomorpha and Scolopendromorpha), and apparently unexpressed in the dense, multifurcating spine field of the Haarpolster of *Craterostigmus*.

Symphyla

The mandibular gnathal edge is described and illustrated in the scutigerellid *Hanseniella* by Richter *et al.* (2002). To briefly summarise the relevant details, a *pars incisivus* and *pars molaris* are readily identified, a differentiation enhanced by the two parts lying on separate sclerites (Fig. 1). The *pars incisivus* forms a narrow, dentate blade (with four cusps in a single file), that occupies the entire distal extent of the gnathal edge. The *pars molaris* is developed as a molar plate, with a row of blunt lobes distally and a generally flattened surface covered with closely-packed tubercles proximally (Fig. 3H). The anterior margin of the *pars molaris* bears narrow ridges separated by sharp grooves. At the distal edge of the sclerite bearing the *pars molaris*, is a multiramous element that has previously been compared to a *lacinia mobilis* (e.g. Snodgrass 1950). A small cluster of spines lies at the proximal end of the *pars molaris* (Fig. 3H).

Diplopoda

The gnathal edge of diplopods has been described and illustrated in several SEM studies [e.g. Enghoff (1979) for Julida; Ishii (1988) for Polyxenida; Köhler & Alberti (1990) for several orders; Ishii & Tamura (1995) for most orders; Ishii & Tamura (1996) for Polydesmida]. The *pars molaris* is represented by a so-called molar plate in Diplopoda (except for Colobognatha: see Enghoff 1984, figs 1–3). Its numerous elaborations in the different orders are summarised by Ishii & Tamura (1995) (see their fig. 1 for micrographs of the *pars molaris* in seven orders and its absence in Colobognatha).

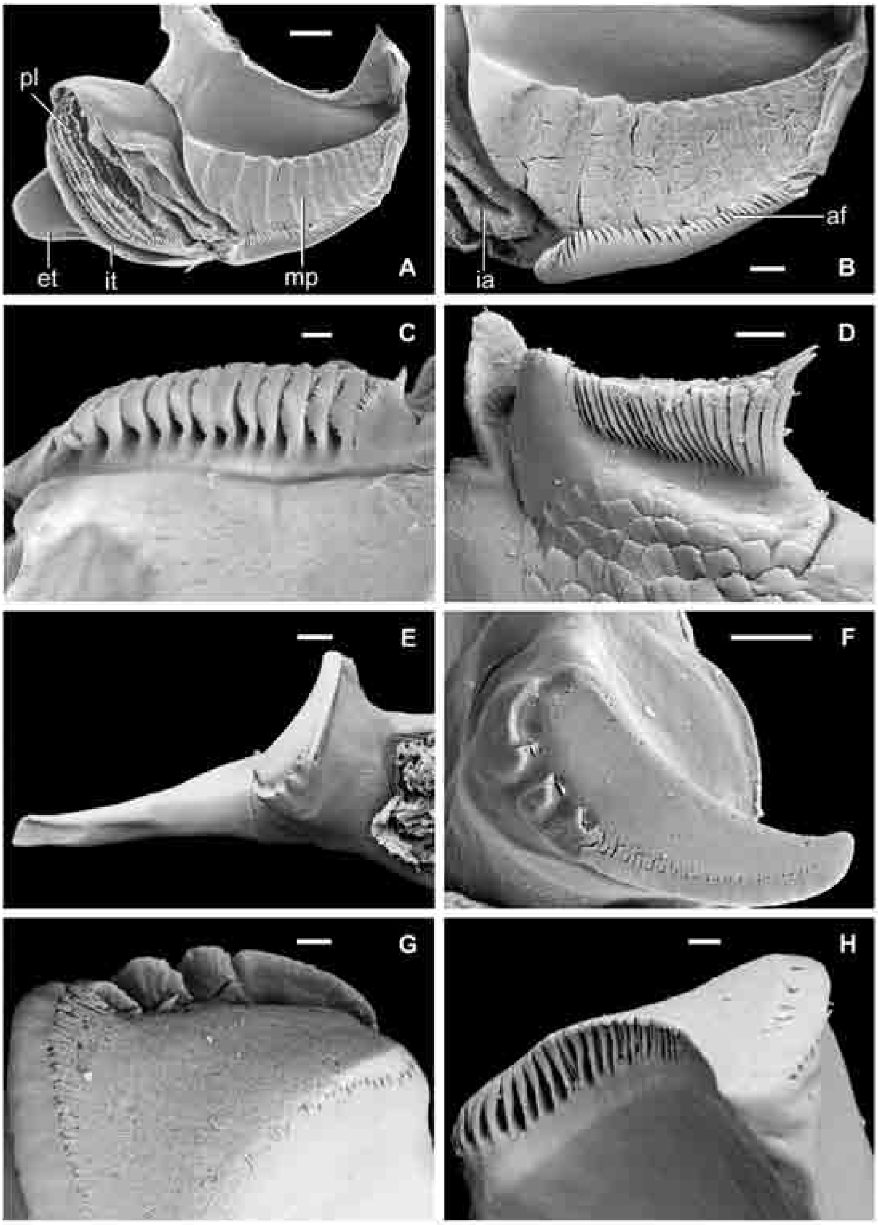

Fig. 4. Mandibular gnathal edge in Diplopoda (A–C) and Hexapoda (D–H). A–B. *Cladethosoma clarum* [Polydesmida, Paradoxosomatidae]. Left mandible, gnathal edge, medial view and detail of molar plate, showing external tooth (et), internal tooth (it), pectinate lamellae (pl), molar plate (mp), intermediate area (ia) and anterior fringe (af), scales 100 µm, 50 µm. C. *Unixenus mjobergi* [Penicillata]. Right mandible, molar plate, anterior view showing serrate limbs (*sensu* Ishii 1988), scale 5 µm. D. *Ctenolepisma* sp. [Zygentoma, Lepismatidae]. Right mandible, *pars molaris*, posterior view, scale 10 µm. E–H, *Nesomachilis howensis* [Archaeognatha, Meinertellidae]. E–G. Left mandible. H. Right mandible. E. *pars incisivus* and *pars molaris*, anteromedial view, scale 50 µm. F. *pars molaris*, medial view, scale 50 µm. G–H. *pars molaris*, proximomedial and proximoposterior views, scales 10 µm.

Following their terminology, the molar plate of diplopods (Figs 4A, B) includes a fringe (densely arranged spines along the anterior margin or both margins of the molar plate; af, Fig. 4B), molar concave (a crescentic or ovoid field at the distal end of the molar plate), salivary ostioles (variably present), and rows of transverse ridges that the authors call molar processes (an unfortunate choice of terminology given the more common usage of 'molar process' in Insecta and Crustacea). A cluster of slender spines called a molar tuft (Ishii & Tamura 1995) is variably present, proximal to the molar plate.

The distal (presumed incisor) part of the gnathal edge in Diplopoda has complex substructures. The incisor region of diplopods (Fig. 1) consists of a comb lobe in Penicillata (Ishii 1988), and the external tooth, internal tooth, and pectinate lamellae [terminology after Enghoff (1979)] in Chilognatha (Fig. 4A). In polyxenids, the comb lobe forms a strongly protruding region distally on the gnathal edge (Ishii 1988, figs 1, 2, 4; Ishii & Tamura 1995, figs 2A, B; Richter *et al*. 2002, fig. 49), strongly separated from the molar plate. This pronounced separation of the (distal) comb lobe and (proximal) molar plate is reminiscent of some incisor and molar processes in insects and crustaceans. Between the comb lobe and molar plate of diplopods is a field called the intermediate area (Enghoff 1979; ia, fig. 4B). Its modifications in diplopods, such as the 'intermediate lobe', 'intermediate sensilla' and 'fimbriate lamella' of Penicillata (Ishii 1988), are so unique that no homologies with structures between the *pars incisivus* and *pars molaris* in other mandibulates have, to our knowledge, been suggested, nor are we able to assign the intermediate area to either the *pars incisivus* or the *pars molaris*.

Richter *et al*. (2002) compared the comb lobe of Penicillata and the distal part of the mandible in Chilognatha, and suggested that the internal and external teeth in Chilognatha are modified pectinate lamellae. This suggestion was based on a serial transformation in the structure of the comb teeth in Penicillata, such that the posteriormost comb teeth in the comb lobe are composed of only a few cusps, coming to resemble the identically positioned internal and external tooth in chilognathans. If this homology is followed, then the *pars incisivus* of Diplopoda primitively consisted of pectinate lamellae (=comb teeth) only, and the internal and external tooth are novel structures for Chilognatha, not homologous with incisor teeth or *laciniae mobiles* in other mandibulates.

Before the Pauropoda can be soundly integrated, Hexamerocerata, which have an articulated gnathal lobe as in Diplopoda (Hüther 1968; Kraus & Kraus 1994, figs 16, 17), require description of their gnathal edge.

Summary of Myriapoda

Figure 1 summarises the proposed homologies and inferred modifications of the *pars incisivus* and *pars molaris* in Myriapoda. Pectinate lamellae are ubiquitous in Diplopoda except within Colobognatha, and are present in all non-geophilomorph Chilopoda. They are probably fundamentally present in Geophilomorpha as well, since multiple comb rows are seen in Mecistocephalidae (sister group to all other geophilomorphs, the clade Adesmata; Minelli *et al*. 2000; Edgecombe & Giribet 2002) and in the adesmatan taxa Himantariidae and Oryidae. The pectinate lamellae have no apparent homologue in Symphyla. If the pectinate lamellae of Chilopoda and Diplopoda are homologous (as is suggested by their positional and structural similarity), then they are likely to be fundamental for Myriapoda, and their absence in Symphyla has to be interpreted as a loss.

A molar plate in the *pars molaris* is present in most orders of Diplopoda, in Symphyla, and in Scutigeromorpha within the Chilopoda. In Symphyla and Scutigeromorpha, the molar plate is developed on a separate sclerite from the *pars incisivus* and has a densely tuberculate surface. The surface of the molar plate has complex (ingroup) modifications in Diplopoda, such as the salivary ostioles and molar concave, whereas structures common to Symphyla and Scutigeromorpha may be basic for Myriapoda. For example, along with the tuberculate surface of the molar plate (Figs 2F, 3H), its anterior edge bears a series of confluent elongate ridges in Symphyla (Richter *et al.* 2002, fig. 44) as well as in Scutigeromorpha (Fig. 2H). In Scutigeromorpha, as argued above, these ridges appear to be bristle or spine-derived (fused bristles). The molar plate in many diplopods has a regularly structured anterior fringe of spines (Fig. 4B) or so-called serrate limbs in Penicillata (Fig. 4C). Other diplopods have a spinose fringe along both anterior and posterior margins of the molar plate (Ishii & Tamura 1995: Glomerida - fig. 1C; Spirostreptida – fig. 1F). A cluster of spines or bristles at the proximal edge of the mandible is shared by symphylans and diplopods (the latter being the molar tuft).

Hexapoda

The hexapod ground-pattern is estimated with reference to basal Insecta (Archaeognatha and Zygentoma), Ellipura (Collembola), and Diplura.

Archaeognatha

Mandibles of Archaeognatha have a tapering, strongly projecting, *pars incisivus* that is widely separated from a large *pars molaris* (Fig. 4E). The teeth on the *pars incisivus* have a few blunt cusps arranged in a single row or wear down to a blade-like tip (Fig. 4E). The *pars molaris* is crescentic on both mandibles. Its surface is weakly concave and densely perforate (Fig. 4F), with rows of flat-topped spines developed inside a smooth band along its anterior edge (Fig. 4G). In *Nesomachilis howensis*, both mandibles have two or three large, blunt cusps along the anterodistal margin of the *pars molaris* (Fig. 4G). The posterior margin of the right mandible has spine rows with open gaps at the marginal fringe (Fig. 4H), with only the bases of the corresponding (posterior marginal) spines being seen on the left mandible (Fig. 4G).

Other representatives of Archaeognatha (*Dilta*: Fürst von Lieven 2000, fig. 2; *Machilis*: Koch 2001, fig. 24) deviate little from the above observations on *Nesomachilis*.

Lepismatidae and Lepidotrichidae

The gnathal edge of *Lepisma saccharina* Linnaeus, 1758 (Koch 2001, figs 29–32) and *Ctenolepisma* sp. is dominated by the *pars incisivus*, which consists of a row of teeth (two distal teeth, a large, multicusped third tooth, and a small, bicusped proximal tooth). The *pars molaris* is a small, narrow, tear-drop shaped pad with small scales on its surface (Koch 2001, fig. 30), lying immediately proximal to the last tooth in the *pars incisivus*. A fringe of slender, simple spines with open gaps between the rows encircles the *pars molaris*. In *Ctenolepisma*, the fringe opens on the posterior edge of the *pars molaris* on the right mandible (Fig. 4D) and opens on the anterior side on the left mandible. A group of spinose setae is situated at the proximal edge of the mandible, proximal to the *pars molaris* (Koch 2001, fig. 32). A few of these setae have bifurcate tips.

The *pars molaris* is relatively larger in the lepidotrichid *Tricholepidion gertschii* Wygodzinsky, 1961 (Staniczek 2000, figs 24, 25, 27) than in Lepismatidae, and the *pars incisivus* is accordingly shorter (composed of three teeth). The shape of the *pars molaris* is, however, similar to that of lepismatids, and in both groups the *pars molaris* lies immediately proximal to the last, small tooth of the *pars incisivus*. In *Tricholepidion*, as in Lepismatidae, a fringe of simple, elongate spines opens on the posterior (inner) edge of *the pars molaris* on the right mandible, likewise extending along the entirety of the *pars molaris* (Staniczek 2000, fig. 27). These similarities in the *pars molaris* and its common masticatory edge with a file of teeth in the *pars incisivus* are either general for Zygentoma or Dicondylia, depending on whether or not *Tricholepidion* is resolved as sister group of the remaining zygentomans Lepismatidae + Nicoletiidae (Kristensen 1998), or as sister group of all other Dicondylia (Staniczek 2000, fig. 30).

Collembola

Comparison with the gnathal edge in other mandibulates is limited to the 'biting-chewing' type of mandible, regarded as plesiomorphic for Collembola (Koch 2001); other collembolans have the mandible modified for fluid-feeding, or even absent. The 'biting-chewing' mandibles have an apical tooth row (the teeth arranged in a single file), positionally and structurally corresponding to a *pars incisivus*. More proximally is a *pars molaris* which has been described as a molar hook (*Tomocerus*: Kraus 1998, fig. 22.1) or molar plate (Koch 2001, figs 9, 10). The *pars molaris* in *Tomocerus* has regularly ordered rows of round tubercles over its entire surface (Kraus 1998, fig. 22.1b), and is fringed anteriorly by a single row of slender spines that grade distally into cusps. The collembolan *pars molaris* resembles the molar plate of Scutigeromorpha in having ordered tubercle rows on its surface, and is similar to the *pars molaris* of many other mandibulates in having an anterior spine fringe.

Diplura

In Campodeoidea (*Campodea*: Koch 2001, figs 15–17; Richter *et al*. 2002, fig. 45), as well as in Japygidoidea (*Anajapyx*: Pagés 1997, fig. 32; *Catajapyx*: Koch 2001, fig. 22), a terminal, multicusped 'shovel' is a dentate process at the distal end of the mandible that is identified as a *pars incisivus* based on its position and dentate form. A *pars molaris* is lacking in Diplura. Koch (2001) suggested that it may be represented by a hump-like projection, though this weak swelling has none of the typical features that serve to identify this region.

Summary of Hexapoda

Though a *pars molaris* is lacking in Diplura, shared details of the *pars molaris* of Collembola, Archaeognatha, Lepismatidae and Lepidotrichidae indicate that a differentiated *pars molaris* can be assigned to the common ancestor of Hexapoda. A dentate *pars incisivus* is present in all of these taxa as well as in Diplura, and can confidently be ascribed to the hexapod ground-pattern. The *pars molaris* of exemplar Collembola and Archaeognatha has a surface composed of rows of spine tips, and the anterior margin of the *pars molaris* in both groups has a single row of cusps along the distal edge. A fringe of marginal spines with open gaps between the spine rows is found along the anterior edge of the mandible in Collembola, with a similar fringe along the posterior margin in Archaeognatha, and along either the anterior or posterior margin (left and right mandibles, respectively) in Lepismatidae. The extreme elongation of the *pars incisivus* is autapomorphic for Archaeognatha.

Crustacea

Representatives of the Malacostraca, Branchiopoda, and Remipedia have mandibles with gnathal edges comprising a distinct *pars molaris* and *pars incisivus* (molar and incisor processes, respectively, in the carcinological literature), and in some cases additional structures inbetween (often called 'spine rows' and *laciniae mobiles*). On the other hand, representatives of the maxillopodan taxa possess different and probably highly derived mandibles, the gnathal edges of which cannot directly be compared with those of the other taxa (see e.g. Olesen 2001 for Mystacocarida, Schnack 1989 for Copepoda, Newman 1996 for Cirripedia). For the Cephalocarida, the gnathal edge of *Hutchinsoniella macracantha* Sanders, 1955, has been described as comprising a grinding molar plate covered with numerous tiny papillae and an incisor process of two spines with a movable bristle inbetween (Sanders 1957). Another species, *Hampsonellus brasiliensis* (Hessler & Wakabara 2000, fig. 3C), shows a similar pattern. We will deal with the other taxa in more detail.

Remipedia

Based on the descriptions by Schram *et al.* (1986), Schram & Lewis (1989), and Richter *et al.* (2002), a general pattern of remipede mandibles can be described. The mandibular gnathal edge consists of a strong *pars incisivus* carrying three (right side) or four (left side) teeth oriented at a right angle to the remaining edge, a similarly strong '*lacinia mobilis*' (not homologous with the peracarid structure; see Richter *et al.* 2002) oriented parallel to the *pars incisivus*, and a *pars molaris*. Schram & Lewis (1989) described a distinct asymmetry in the Speleonectidae and only slight asymmetry in the Godzilliidae, although the general pattern is the same in both families. The asymmetry concerns the shape of the *pars incisivus* as well as that of the *lacinia mobilis*, but not that of the *pars molaris* (e.g. Richter *et al.* 2002, figs 37–38). In *Speleonectes* cf. *tulumensis* (Fig. 5A–B), the elongated *pars molaris*, which covers about half of the entire gnathal edge, consists of two densely packed rows of about 50 lamella-like spines each. The spines decrease in length and width towards the proximal end of the gnathal surface. The spines are neither confluent with anterior nor with posterior projections of the gnathal surface, so fringes of spines are present on both sides. This general pattern holds true for other Remipedia (Schram *et al.* 1986; Schram & Lewis 1989).

Branchiopoda

Branchiopod mandibles are large appendages lacking a palp in the adults. The distal portion of the mandible carrying the gnathal edge is separated from the proximal portion by an abrupt, distinct medial curve. Within the Branchiopoda, representatives of the Anostraca, Spinicaudata, Cyclestherida and Cladocera possess triturating surfaces consisting almost exclusively of a *pars molaris*. The gnathal edge of the mandibles in Notostraca and Laevicaudata carries a row of large teeth quite unlike a typical *pars molaris*. Their mandibles have been interpreted as derived (Cannon 1933; Linder 1941). The same is true for the mandibles of the predatory Cladocera (Rivier 1998). Here, we will focus on the mandibles of the remaining taxa.

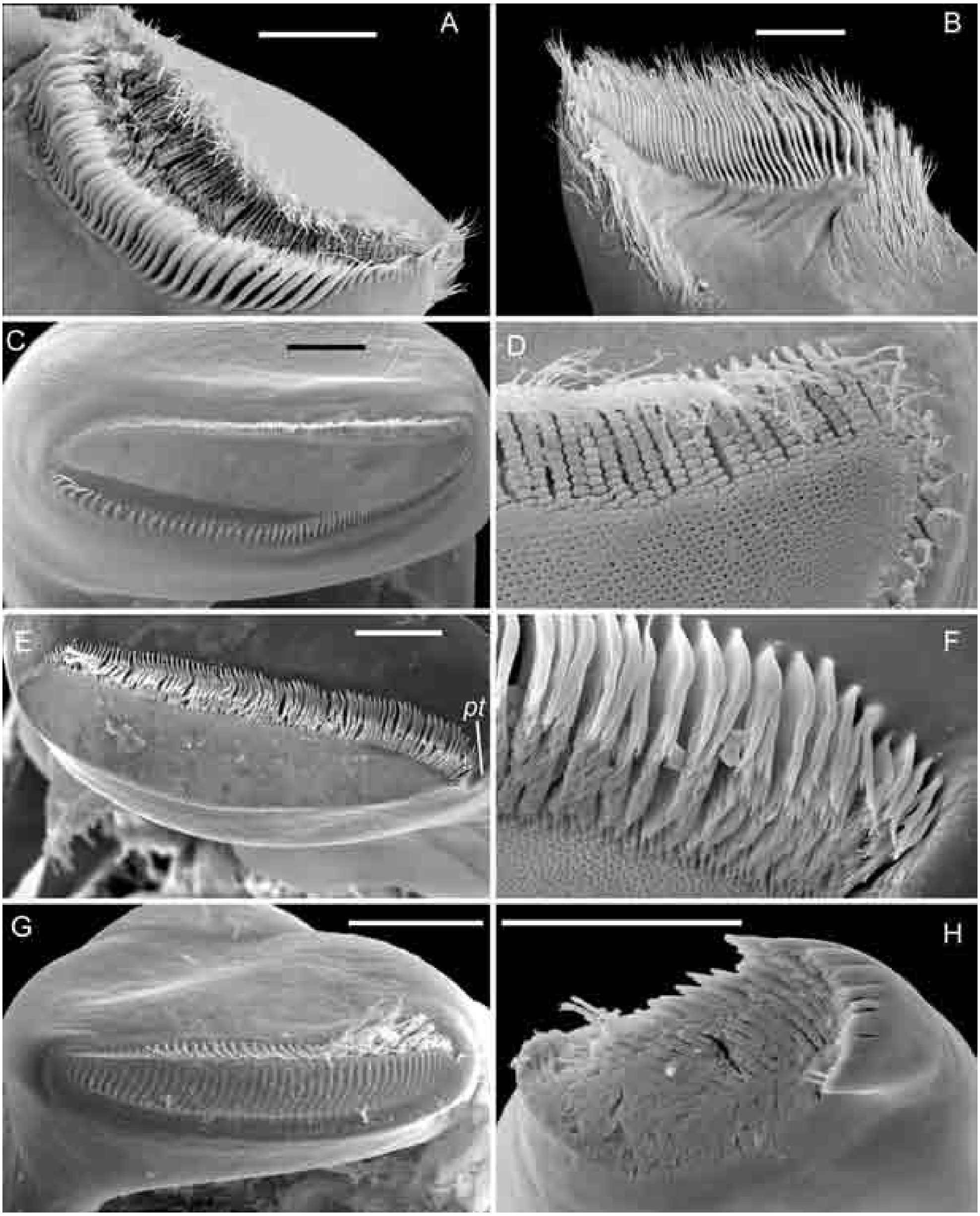

Fig. 5. Mandibular gnathal edge in Crustacea. A–B. Remipedia. C–H. Branchiopoda, medial views. A–B. *Speleonectes* cf. *tulumensis* [Speleonectidae], left mandible, anterior and posterior views, respectively, scale 50 µm. C–D. *Branchinella pinnata* [Anostraca, Thamnocephalidae], right mandible with enlargement of surface adjacent to mouth, scale 100 µm. E–F. *Limnadopsis birchii* [Spinicaudata, Limnadiidae], left mandible showing posterior tooth (pt), with enlargement of surface opposite to mouth, scale 100 µm. G. *Cyclestheria hislopi* [Cladoceromorpha, Cyclestheridae], right mandible, scale 50 µm. H. *Eurycercus glacialis* [Cladocera, Chydoridae], right mandible, scale 100 µm.

The gnathal surfaces of various anostracans have been documented using SEM (e.g. (Mura 1995 1996). In general, they are similar throughout the different families, the *pars molaris* almost covering the entire edge (Fig. 5C). The surface of the *pars molaris* is formed by cuticular projections (spines) of the gnathal edge. These spines are elongated, comb-like structures. The common 'comb basis' originates from the primary level of the gnathal edge, the 'comb teeth' form a second, more distal layer, the visible surface of the *pars molaris*. In the central region of the molar surface, the 'teeth' are confluent and build a smooth surface (plate) that is perforated by numerous small pores (Fig. 5D). Typically, the spines although densely packed, are separated from each other at the edges of the *pars molaris* (anteriorly, posteriorly, or on both sides, also depending upon whether the left or right mandible is under consideration). As a result, a fringe of spines with open gaps between the spine rows (herein called 'open fringe') is present. In *Branchinella pinnata*, the open fringe is present on the anterior edge (i.e. the edge orientated ventrally, towards the labrum) of the left mandible and on the anterior edge and parts of the posterior edge of the right mandible (Fig. 5D). A similar pattern is found in other anostracan species (Mura 1995 1996). In some species, large teeth are present at the posterior (i.e. distal in comparison to the other taxa discussed herein) tip, e.g. in the predatory *Branchinecta ferox* (Milne-Edwards, 1840) (see Fryer 1983). Whether these teeth can be related to a *pars incisivus*, which corresponds in the distal position, seems doubtful. Fryer (1983) and Mura (1995) convincingly argued that these teeth can be related to a predatory feeding habit (which, however, does not exclude their homology with a *pars incisivus*).

The mandibles of the Spinicaudata, Cyclestherida and certain Cladocera are similar to those of the Anostraca. Martin (1989) described and documented the gnathal surfaces of one representative of each of the families, Cyzicidae, Leptestheriidae and Limnadiidae, and also included *Cyclestheria hislopi* (probably the sister group to the Cladocera, see e.g. Ax 1999). As in the Anostraca, the gnathal edge is almost entirely covered by the *pars molaris* (Fig. 5E, *Limnadopsis birchii*, G, *Cyclestheria hislopi*, H, *Eurycercus glacialis*). Its surface is built by confluent rows of spines forming a grinding plate. In *Limnadopsis birchii* (Limnadiidae), these spines are comb-like, with the connecting part proximally and the 'comb teeth' distally. The central region of the molar surface is relatively smooth and perforated with numerous small pores. On the left mandible (Figs 5E, F), the spines are confluent with the gnathal edge at the posterior and lateral sides, but have gaps opening to the anterior (ventral) sides. An open fringe of spines is clearly visible on the anterior side. The right mandible is different: the open fringe is present at the posterior side. Both mandibles have a distinct posterior tooth (Fig. 5E, pt) that might represent the *pars incisivus*. This tooth is also present in *Leptestheria compleximanus* (Packard, 1877) (Martin 1989, fig. 3F). Walossek (1993) described the mandibles and their development in the Upper Cambrian branchiopod *Rehbachiella kinnekullensis* Müller, 1983. Later stages (see his figs 17 F & G; plate 28:2) have an anterior (proximal) *pars molaris* (broadened and concave area) and several teeth representing the posterior (distal) *pars incisivus*, both parts covering about half of the gnathal edge each. This weakens Manton's suggestion (1964 1977) that the anostracan mandible consisting exclusively of a *pars molaris* represents the ancestral stage for the Crustacea. Considering *Rehbachiella*, this hypothesis might not even be true for the Branchiopoda.

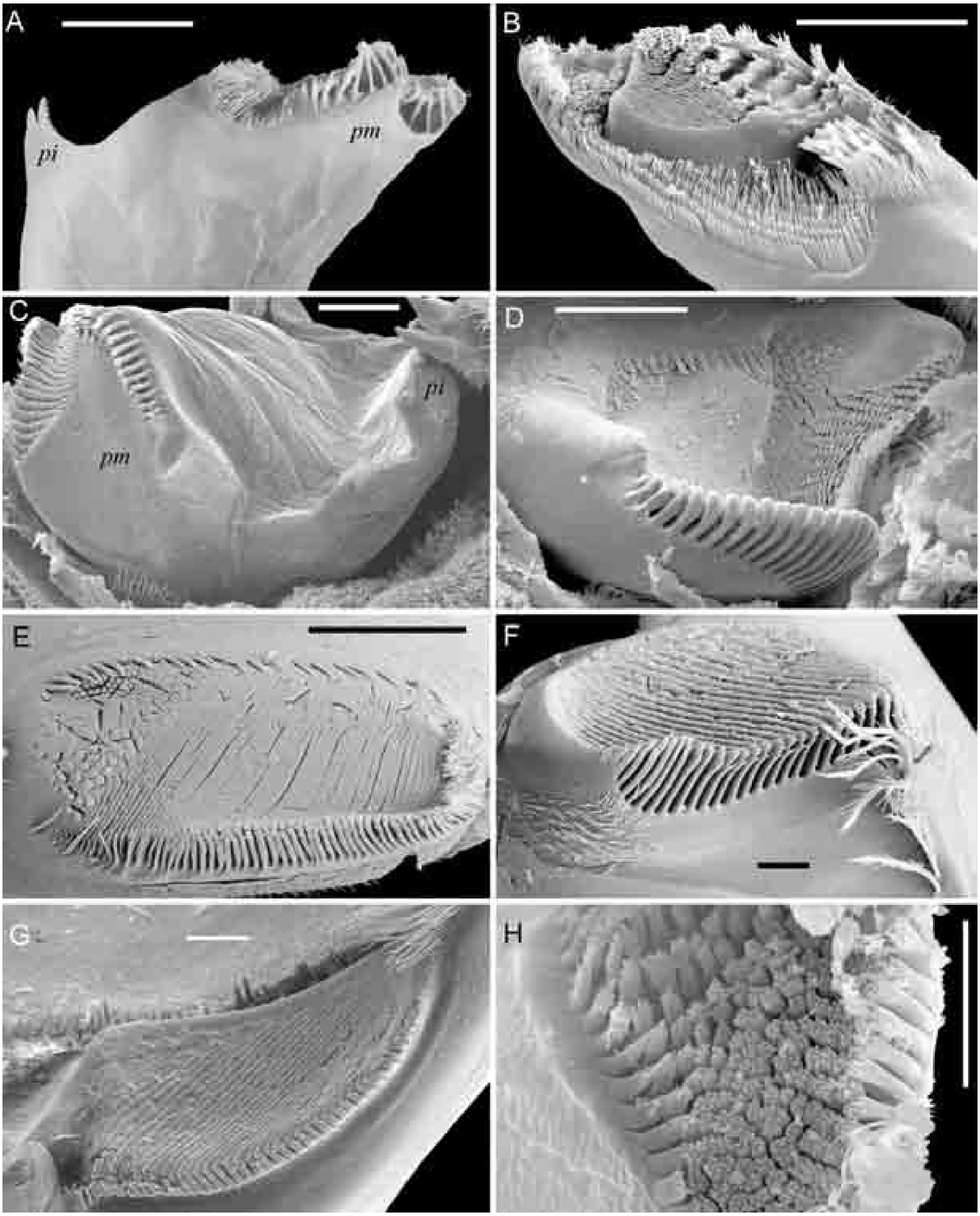

Fig. 6. Mandibular gnathal edge in Malacostraca, showing *pars incisivus* (*pi*) and *pars molaris* (*pm*). A–B. *Paranebalia* sp. [Leptostraca, Paranebaliidae], left mandible, anterior (ventral) view, and *pars molaris* enlarged, distomedial view, scale 50 µm. C–D. *Meganyctiphanes norvegica* [Euphausiacea, Euphausiidae], left (C) and right (D) mandibles, respectively, medial views, scales 100 µm. E. *Anaspides tasmaniae* [Syncarida], left *pars molaris*, anteromedial view,scale 50 µm. F. *Peludo paraliotus* [Isopoda, Phreatoicidea], left *pars molaris*, anterior view, scale 50 µm. G. *Gnathophausia zoea* [Lophogastrida, Lophogastridae], right *pars molaris*, medial view, scale 100 µm. H. *Tethysbaena argentarii* [Thermosbaenacea, Monodellidae], left *pars molaris*, medial view, scale 10 µm.

Malacostraca

We endorse Koch's (2001: 165) conclusion that 'the presence of both a distinct *pars molaris* and a *pars incisivus* with certainty belongs to the ground pattern of the Malacostraca'. Interestingly, the apparent *pars incisivus* in most representatives of the Leptostraca is extremely weak (*Paranebalia*, Fig. 6A; *pi*, and in *Nebalia* species; but not in *Nebaliella*, see Cannon 1960, figs 9A–E), as opposed to the Eumalacostraca where most taxa have a well developed *pars incisivus* (Richter *et al*. 2002; e.g. Euphausiacea, fig. 6C; *pi*). The apparent leptostracan *partes incisivi* do not even meet medially, and thus resemble spines on the exterior lateral margin of the mandible. The *pars molaris* of *Paranebalia* (Figs 6A–B) is large and more complex in construction than in most Eumalacostraca (Figs 6C–H), with a central molar region with anterior spines grading posteriorly into ridges, surrounded by an hemicircular shelf of fine rows of cuticular hairs or spinules (Fig. 6B), with open gaps in the rows on the anterior side. Whether this shelf represents a specialisation of the molar surface within the Leptostraca or a basal feature of the Malacostraca is uncertain. The *pars molaris* of most Eumalacostraca shows open-gapped spine rows merging into a ridged medial surface (Euphausiacea, Figs 6C–D; Anaspidacea, Fig. 6E; Isopoda, Fig. 6F; Lophogastrida, Fig. 6G). In representatives of the Euphausiacea (Figs 6C–D; see also De Jong-Moreau *et al*. 2001, fig. 4), and in the peracarid taxa Lophogastrida (Fig. 6G) and Mysida (e.g. De Jong-Moreau *et al*. 2001, figs 1–3; Richter *et al*. 2002, figs 1, 3), the open fringe of spines lies anteriorly on the left mandible, and posteriorly on the right mandible, whereas in Anaspidacea (Fig. 6E) and in Isopoda (Fig. 6F), the fringe has gaps that are open anteriorly on both mandibles. In other Eumalacostraca, such as the thermosbaenacean *Tethysbaena argentarii* (Fig. 6H), the spines are stout single elements that do not merge into ridges. Here, the open fringe of spines surrounds the entire *pars molaris*.

Summary of Crustacea

The presence of a distinct *pars molaris* and *pars incisivus* in Cephalocarida, Remipedia, Malacostraca, and in the proposed ground-pattern of the Branchiopoda (based on *Rehbachiella*) argues for these features belonging to the crustacean ground-pattern. Despite differences in detail, the *pars molaris* in Crustacea is formed by rows of lamella-like spines that often form ridges on the surface of the *pars molaris*. In some taxa (in particular Malacostraca and Branchiopoda), the spines are confluent with the posterior and lateral projections of the gnathal edge, which results in a fringe of spines with open gaps only on the anterior side. Several taxa show a distinct asymmetry in the *partes molares* where, in contrast to the general pattern, the spines of the right mandibles are confluent with anterior projections of the gnathal edge. The gaps in the fringe rows then appear on the posterior side on the right mandible. The distribution of these two patterns does not permit a certain decision about which of them belongs to the crustacean ground-pattern.

GENERAL DISCUSSION

Taxa across each of the Myriapoda, Hexapoda and Crustacea exhibit common aspects of the structure of the mandibular gnathal edge. The distal margin of the mandible is dentate in myriapods (notably Symphyla), hexapods [including Collembola, Diplura, Archaeognatha and Zygentoma; also basal Pterygota (Staniczek 2000)], and in the crustaceans Remipedia, Cephalocarida and Malacostraca. The most elaborate modifications of a dentate *pars incisivus* are seen in Diplopoda and Chilopoda, where a series of pectinate lamellae occupies the distal part of the gnathal edge (Chilopoda and Penicillata), or is enclosed by the internal and external tooth (Chilognatha). By comparison to crustaceans and hexapods, the comparatively simple row of teeth in the *pars incisivus* in Symphyla could be regarded as plesiomorphic.

Structural details of the *pars incisivus* and *pars molaris* in various mandibulate taxa provide corroboration for the basic homology made using positional correspondence (i.e. distal and proximal sections of the gnathal edge). The *pars incisivus* in members of Myriapoda, Hexapoda and Crustacea is a blade-like process with a row of teeth. The *pars molaris* typically has a flattened surface, displaying evidence for an origin by confluence of spines that are arranged in rows. This means that the functional surface of the *pars molaris* does not represent the original surface of the gnathal edge, but constitutes a second more distal layer. It is fringed by a row of spines that typically have open gaps between the rows on one side of the *pars molaris*, and has a cluster of spines or bristles proximal to a molar plate or process. These details of structure, combined with the distribution of the *pars incisivus* and *pars molaris* in the major lineages of Myriapoda, Hexapoda and Crustacea, lead us to favour a general homology of these elements in mandibulates, and thus their presence in the common ancestor of the Mandibulata. Kraus (1998) previously suggested that the *pars molaris* ('Molar hooks' in his terminology) is a decisive autamorphy of the Tracheata, and later (Kraus 2001) extended the homology to the *pars molaris* of Crustacea and regarded it as an autapomorphy of the Mandibulata. Several questions warrant further consideration. For example, the systematic distribution of the open-gapped spine fringe on the anterior or posterior edge of the *pars molaris* is difficult to reconstruct for the ground-patterns of Crustacea and Hexapoda in particular. The significance of asymmetries in various branchiopods, eumalacostracans and lepismatids (fringe opening anteriorly on the left mandible and posteriorly on the right mandible) is likewise uncertain.

If a *pars molaris* and *pars incisivus* are basic for Myriapoda, Hexapoda and Crustacea, this complex differentiation of the gnathal edge can be regarded as an additional indication for a single origin of the mandibles (and monophyly of Mandibulata). The concept of a mandible could be expanded to include segmental identity (appendage of the cephalic metamere with post-tritocerebral innervation), functional role (anteriormost mouthpart of the adult head, biting with a coxal endite), topological relationships to other components of the head capsule (embedding in a chewing chamber beneath the labrum), gene expression patterns (lack of *Distal-less* expression along the inner margin of the mandible; gradient of decreasing *Distal-less* expression in ontogeny), and the differentiation of the gnathal edge into a distal, dentate *pars incisivus* and a proximal *pars molaris*, of which a molar plate is the fundamental component. The latter has a surface built by confluent rows of spines. These arguments lead us to endorse Snodgrass' (1938) classical grouping of myriapods, hexapods and crustaceans on the basis of their unique mouthpart, the mandible.

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